

THE GENERA PROPLEOPUS AND HYPSSIPRYMNODON AND  
THEIR POSITION IN THE MACROPODIDAE

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Any assessment of the systematic position of the extinct *Propleopus oscillans* (De Vis) depends wholly on comparison with similar parts of the living *Hypsiprymnodon moschatus* Ramsay and related forms. Palaeontological evidence of its affinities is lacking. *Propleopus* Longman was included with *Hypsiprymnodon* Ramsay and *Burramys* Broom in the subfamily Hypsiprymnodontinae of the Macropodidae by Tate (1948). However Ride (1956) has shown conclusively that *Burramys parvus* Broom, known only from fossils of presumed Pleistocene age from Wombeyan Caves, New South Wales, is not a macropodid. He placed it in the subfamily Phalangerinae of the Phalangeridae.

The type of *P. oscillans* is in the collections of the Queensland Museum. De Vis' original description (1888) is erroneous in some features, and many characters are only compared with those in other genera, which themselves have never been adequately described or figured. A redescription and new figure of the type are provided below. It is surprising to find that, while *H. moschatus* has been much discussed in the literature since its original description by Ramsay (1876), no comprehensive account of its dentition has been provided. Indeed the interpretation of Carlsson (1915) of the deciduous teeth will be shown to be erroneous, and these errors have been perpetuated by later authors. Fortunately there is a good series of skulls, including those of juveniles, in the collections of the Queensland Museum, and a description of the dentition of *H. moschatus* is given. The evidence of the dentition and certain other characters in determining the systematic position of *Hypsiprymnodon* is also discussed.

**PROPLEOPUS OSCILLANS** (De Vis)

(Figure 1)

*Triclis oscillans* De Vis, 1888, Proc. Linn. Soc. N.S.W., 3, p. 8, pl. 1.

*Propleopus oscillans* (De Vis). Longman, 1924, Mem. Qd. Mus., 8, p. 20.

MATERIAL.—Type, F. 3302, incomplete left ramus, with I<sub>1</sub>, P<sub>3</sub>—M<sub>4</sub>, King Creek, Darling Downs, S. E. Queensland.

F. 681, left I<sub>1</sub>, Darling Downs, Q. ; F. 3287, cast of incomplete right ramus, with M<sub>1</sub>—M<sub>4</sub>, Wellington Caves, New South Wales (cast of Univ. Calif. Mus. Paleont. No. 45171).

## Redescription of Type

Mandible robust; ventral margin arcuate, with greatest depth below  $M_1$ . Symphysis ligamentary; elongate, extending to point opposite anterior edge of  $P_3$ ; subalveolaris fossa shallow; then prominent postsymphysial swelling (for root of  $I_1$ ). Diastema long; diastemal crest rounded behind alveolus of  $I_2$ , becoming sharper and swinging posterolaterally toward nearly obliterated alveolus of  $P_2$ . Mental foramen large, slightly anteroventral to  $P_2$ . Ramus incomplete posteriorly, but masseteric canal confluent with inferior dental canal and extending to below anterior molars; postalveolar shelf short, triangular, flanked by prominent postalveolar ridge.

$I_1$  rather short, but deeply rooted; slightly curved in lateral view, ascending to extensive subhorizontal surface of wear, gently rounded at tip; rounded-cuneate in transverse section, much higher than wide; enamelled ventrolaterally, with enamel extending half-way laterally, less so mesially; mesial facet of wear towards tip.  $I_2$  missing, but open alveolus small, subhorizontal.

$P_3$  larger than molars, suboval at base of crown; trenchant, with cutting edge oblique, making an angle of about  $20^\circ$  with molar axis; high, ascending anteriorly; surface of wear labial, more conspicuous posteriorly. Lingual and labial faces each with seven nearly vertical, opposed ridges; penultimate anterior pair rising to cuspule slightly above cutting edge; posterior pair short, weaker; anteriorly with median ridge descending, swinging lingually, weakening.

$M_1 < M_2 < M_3 > M_4$ ; molar row straight, converging slightly anteriorly with axis of mandible, displaying pronounced anterolabial roll. Molars brachyodont, subrectangular, more lophoid anteriorly.  $M_1$  broader posteriorly; protoconid low, rounded, with short forelink

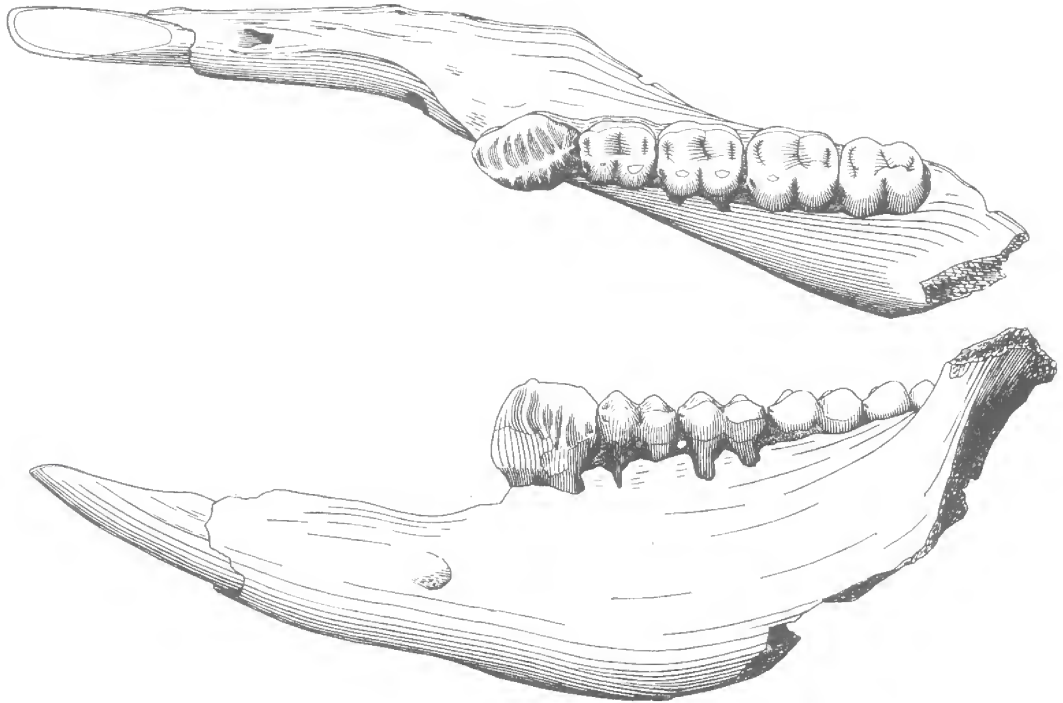


Figure 1.—*Propleopus oscillans* (De Vis). Occlusal and lateral views of left ramus; F.3302, type, natural size.

descending slightly and swinging mesiad to anterior cingulum, and similar posterior projection contributing to low midlink; metaconid high, somewhat trihedral, with labial spur descending to protoconid, forming short protolophid, and with curved lingual face extending from anterior cingulum to tiny stylid in central valley; anterior cingulum descending labially, recurving beyond forelink; hypoconid low, rather crescentic, separated from smaller protoconid by deep labial cleft, posteriorly with hindlink passing to short posterior cingulum; entoconid rather similar to, but lower than metaconid, largely contributing to hypolophid.  $M_2$  with anterior moiety subequal in width to, but longer than, talonid; protoconid and hypoconid low, rounded; metaconid higher than entoconid, both trihedral; hypolophid medianly low, divided.  $M_3$  more distinctly quadrituberculate, wider anteriorly; with few grooves nearly obliterated in floor of lingual part of central valley; hypoconid subequal to entoconid.  $M_4$  displaying greater reduction of talonid, with entoconid inferior to hypoconid, posterior cingulum short; cusps more distinctly separated, especially those of talonid.

Measurements (mm.)

	F.3302 (Type)	F.3287	F.681
$I_1$ in dorsal view .. .. .	22.9 x 6.9		
$I_1$ in section .. .. .	9.8 x 6.9		11.7 x 7.6
Length of Symphysis .. .. .	43		
Tip of $I_1$ to posterior of postsymphysial swelling	76		
Diastema ( $I_1$ - $P_3$ ) .. .. .	39		
$P_3$ .. .. .	13.9 x 9.7		
$M_1$ .. .. .	9.5 x 8.7	9.3 x 9.2	
$M_2$ .. .. .	10.8 x 9.8	10.1 x 10.0	
$M_3$ .. .. .	11.2 x 10.3	10.7 x 10.2	
$M_4$ .. .. .	11.0 x 9.6	10.2 x 8.6	
Depth of ramus below $P_3/M_1$ .. .. .	31	27	

Etheridge (1892) realized that *Triclis* De Vis 1888 was preoccupied by *Triclis* Loew 1851, and Longman (1924) proposed the generic name *Propleopus* to replace the junior homonym.

Fossils of *P. oscillans* are very rare in the Pleistocene fluviatile deposits of the Darling Downs. Among the several hundred macropodid skull fragments in the collections of the Queensland Museum from that area, only one specimen other than the type is referable to this species. This incisor fragment is larger in cross section than that of the type, its surface of wear is longer and slightly concave longitudinally.

The cast of the specimen from Wellington Caves was received in exchange from the Museum of Paleontology of the University of California, and the permission of Professor R. A. Stirton to incorporate remarks on the specimen is gratefully acknowledged. The molars of this ramus are slightly smaller and less worn than those of the type. They are relatively broader in the anterior moiety, especially that of  $M_1$ , and the anterior cingulum of this tooth is inconspicuous on its labial development

beyond the forelink. In addition,  $M_4$  shows greater reduction, especially in the talonid. It is impossible to assess the significance of this variation until more material is obtained. A generally similar fossil fauna is obtained from both localities, which are over 400 miles apart. As shown in the table (p.206) there is appreciable variation in the proportions of the teeth of the living *H. moschatus* which has a restricted geographic range.

Tedford (1955) recorded the genus *Propleopus* from the lowest unit of the archaeological site at Lake Menindee in New South Wales. This unit contains evidence of human occupation, and a mixture of living and extinct mammalian genera. Tedford suggested a late Pleistocene or early Recent age for these remains.

#### HYPSIPRYMNODON MOSCHATUS Ramsay

(Figures 2-4)

*Hypsiprymnodon moschatus* Ramsay, 1876, Proc. Linn. Soc. N.S.W., 1, p. 34.

*Pleopus nudicaudatus* Owen, 1877, Ann. Mag. Nat. Hist., ser. 4, 20, p. 542.

MATERIAL.—The account of the dentition is based on the following skulls in the collections of the Queensland Museum : J. 145, ♂, Yungaburra, N. E. Queensland ; J. 5932, ♂, N. E. Queensland ; J. 6824, Lake Barrine, N. E. Queensland ; J. 6826, ♂, Lake Barrine, N. E. Queensland ; J. 10230, juvenile, N. E. Queensland ; J. 10231, juvenile, Cardwell, N. E. Queensland ; J. 10232, juvenile, N. E. Queensland ; J. 10233, ♀, Cardwell, N. E. Queensland ; J. 10234, ♀, Cardwell, N. E. Queensland ; J. 10235, ♂, Cardwell, N. E. Queensland ; J. 10236, ♀, Cardwell, N. E. Queensland ; J. 10237, ♂, Cardwell, N. E. Queensland.

According to Tate (1952) this rain-forest species ranges from near Helenvale, south of Cooktown, to Mt. Spec, near Paluma, north-west of Townsville, in north-eastern Queensland.

#### Dentition

$$\text{Dental formula : } I \frac{1.2.3}{1.2.0} \quad C \frac{1}{0} \quad P \frac{0.2.3}{0.2.3} \quad M \frac{1.2.3.4}{1.2.3.4}.$$

Upper incisors in anteriorly convergent rows.  $I^1$  largest, axially curved ; directed anteroventrally and somewhat mesiad, with tips approximated in some juveniles ; labial surface curved, but flatter distally ; plane of wear ascending to that of  $I^{2-3}$ , but anterior edge progressively rounded off in later life.  $I^2$  erupted before  $I^1$  and  $I^3$  ; crown short, but expanded, elongate oval in occlusal view, excavated and carrying enamel papillae ; wearing with  $I^3$  to form subhorizontal step.  $I^3$  with higher but narrower crown than  $I^2$  ; labial face rather flattened, slightly excavated distally in unworn examples.

C small, separated from I<sup>3</sup> by short diastema; axially curved, somewhat anteroventrally directed; laterally compressed; distal edge sharp, longitudinally rounded.

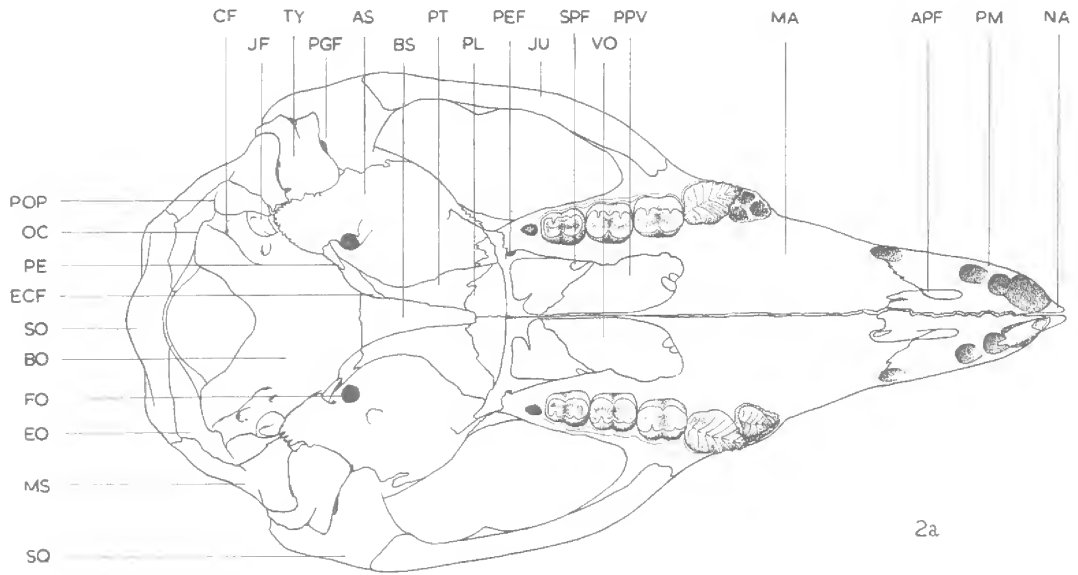
P<sup>2</sup> separated from C by longer diastema; emplaced after DP<sup>3</sup>; trirooted; crown small, subcordate in occlusal view; trenchant, with secant edge initially longitudinal, later swinging slightly anterolabially, serrated, higher posteriorly; lingual and labial faces each with five nearly vertical, opposed ridges; and sixth rounded posterior lingual ridge descends to short, low lingual cingulum. P<sup>2</sup> lost shortly after emplacement of P<sup>3</sup>.

DP<sup>3</sup> molariform, but differing in pattern from true molars; trirooted; paracone high, compressed, with sharp longitudinal forelink descending to prominent parastyle in middle of anterior cingulum, and posterior link descending, swinging labially to low mesostyle of variable development; protocone low, crescentic, linguad and slightly posterior to paracone; metacone smaller, slightly lower than paracone, anteriorly descending to mesostyle, posteriorly with short hindlink descending sharply to short cingulum, passing to tiny hypocone; occlusal basin with finely reticulate, ridged enamel surface.

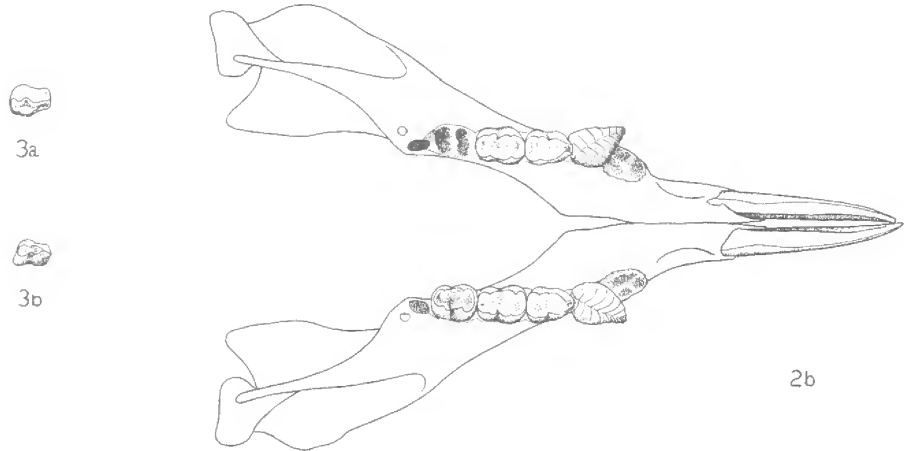
P<sup>3</sup> emplaced before M<sup>4</sup> erupts; birooted, with large oblique posterior root; crown large, high, subcordate in occlusal view; trenchant, with secant edge initially diverging from longitudinal cranial axis by about 22°, later increasing to about 30°, serrate, higher posteriorly; lingual and labial faces each with seven nearly vertical, opposed ridges, with posterior pair weak; and short heavy posterior lingual ridge descending to low lingual cingulum.

M<sup>1</sup> = M<sup>2</sup> > M<sup>3</sup> > M<sup>4</sup>; molar rows parallel in juveniles, appreciably divergent anteriorly later, markedly anisognathous with lower molars, very feebly convex labially; displaying some anterolingual roll; lingual cusps wearing at greater rate. Molars brachyodont, quadrituberculate; trirooted, with single posterior root. M<sup>1</sup> with anterior and posterior moieties equal; paracone high, subconical, with smooth curved labial surface between forelink, descending to small parastyle, posterior link descending to meet anterior link of metacone and delimit central valley; protocone lower than paracone, crescentic, anteriorly passing to short cingulum, posteriorly separated from hypocone by deep lingual cleft, closed at base of crown; metacone rather similar to paracone, but with summit of cusp more distinctly linguad to and transversely linked with crest of smooth labial surface, hindlink descending to wider posterior cingulum; hypocone slightly higher than protocone, but lower than metacone, crescentic, posteriorly passing to cingulum; occlusal basins finely ridged; base of crown expanded. M<sup>2</sup> of similar form to M<sup>1</sup>, but anterior cingulum wider, parastyle weaker; anterior moiety appreciably wider than posterior at base of crown; metacone equal to hypocone; incipient loph formation of descending spurs from opposite cusps. M<sup>3</sup> of lower crown height and greater posterior contraction; metacone slightly reduced; weak loph development, more from labial cusps. M<sup>4</sup> erupted after greater hiatus than those between appearance of anterior molars, reduced, especially posteriorly, subtriangular in outline; metacone vestigial; hypocone small; small parastyle present.

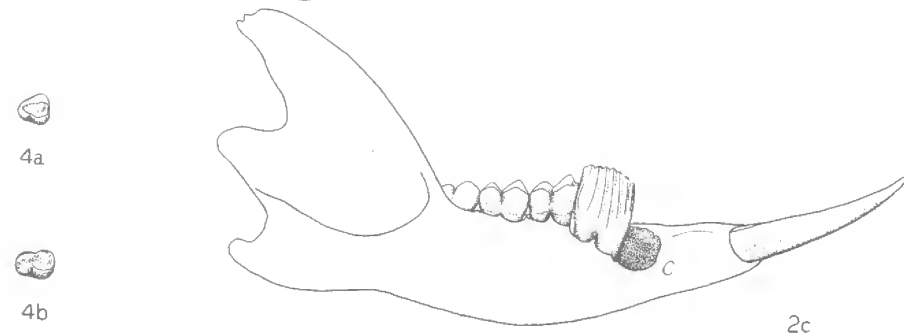
I<sub>1</sub> very long, ascending at low angle, approximated ventrally towards tips, with development of mesial facet of wear; root compressed oval in section; crown subquadrantal at base, tapering and blade-like distally, slightly upcurved and incurved towards tip, with three longitudinal flanges—dorsolabial, ventromesial, and dorsomesial towards base; surface of wear with upper incisors subhorizontal, near planar (by attrition with I<sup>2-3</sup>), with slight rounding of tips (against I<sup>1</sup>). I<sub>2</sub> minute, tubular, anteriorly directed, adpressed to ramus and base of I<sub>1</sub>, not functional and lost at varying stages.



2a



2b



2c

$P_2$  emplaced after  $DP_3$ ; generally similar to  $P^2$ , but without rudimentary lingual cingulum,  $DP_3$  submolariform; compressed, especially anteriorly; metaconid high, in continuation with secant edge of  $P_2$ , with forelink descending to prominent parastylid, sharp hindlink carrying metastylid; protoconid absent, but an inconspicuous labial link descends steeply from metaconid to join crescentic hypoconid; entoconid compressed, anteriorly separated by deep notch from metastylid, posteriorly joined by curved cingulum to lower hypoconid.  $P_3$  generally similar to  $P^3$ , but without lingual cingulum; erupted with secant edge diverging from molar axis by about  $25^\circ$ , increasing later to about  $30^\circ$ .

$M_1 < M_2 > M_3 > M_4$ ; molar rows slightly convergent anteriorly in juveniles, parallel in adults, displaying some anterolabial roll. Molars descending in height posteriorly; birooted; crowns with enamel more extensive labially, but cusps there subject to greater wear.  $M_1$  contracted anteriorly; metaconid compressed, oblique, almost collinear with, but lower than, secant edge of  $P_3$ , short forelink descending steeply via tiny parastylid to high narrow anterior cingulum, labial spur descending to join low arcuate protoconid; entoconid trihedral, with smooth steep lingual surface, labial spur descending to meet corresponding shorter process of hypoconid in incipient lophid development, posteriorly passing to low curved cingulum; hypoconid lower, crescentic, separated from protoconid by prominent labial cleft, closed at base of crown; occlusal basin initially finely ridged.  $M_2$  with anterior moiety much longer and slightly wider than posterior; metaconid trihedral, slightly in advance of lower crescentic protoconid, joined by wide curved anterior cingulum; incipient lophid development.  $M_3$  smaller, but generally similar to  $M_2$ ; hypoconid equal to entoconid.  $M_4$  erupted after longer hiatus than those between appearance of anterior molars; posteriorly reduced.

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Figures 2 4.—*Hypsiprymnodon moschatus* Ramsay.

2a, occlusal view of cranium, showing left  $P^2$ - $M^3$ ; 2b, occlusal view of mandible, showing right  $P_3$ - $M_3$ ; 2c, lateral view of right ramus; J.6824, x 2.

*APF*, anterior palatine foramen  
*AS*, alisphenoid  
*BO*, basioccipital  
*BS*, basisphenoid  
*CF*, condylar foramen  
*ECF*, entocarotid foramen  
*EO*, exoccipital  
*FO*, foramen ovale  
*JF*, jugular foramen  
*JU*, jugal  
*MA*, maxilla  
*MS*, mastoid  
*NA*, nasal  
*OC*, occipital condyle

*PE*, petrosal  
*PEF*, postero-external palatine foramen  
*PGF*, postglenoid foramen  
*PL*, palatine  
*PM*, premaxilla  
*POP*, paroccipital process  
*PPV*, posterior palatal vacuity  
*PT*, pterygoid  
*SO*, supraoccipital  
*SPF*, sphenopalatine foramen  
*SQ*, squamosal  
*TY*, tympanic  
*VO*, vomer

3a, occlusal view of right  $DP^3$ ; 3b, occlusal view of right  $DP_3$ ; J.10231, x 2.

4a, occlusal view of right  $M^4$ ; 4b, occlusal view of right  $M_4$ ; J.10233, x 2.

Measurements (mm.)

Reg. No.	Length (acanthion- inion)	P <sup>2</sup>	DP <sup>3</sup>	P <sup>3</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	M <sup>4</sup>	P <sub>2</sub>	DP <sub>3</sub>	P <sub>3</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>
J.10230	36	r 2.0 x 2.0 l 2.1 x 2.0	2.7 x 2.2 2.7 x 2.0	2.8 x 2.3 2.8 x 2.2	2.9 x 2.4 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	1.8 x 1.6 1.9 x 1.6	2.5 x 1.7 2.5 x 1.6		3.0 x 2.1 3.0 x 2.1			
J.10231	42	r 1.9 x 2.0 l 2.0 x 2.1	2.6 x 2.0 2.6 x 2.0	2.9 x 2.4 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	1.8 x 1.8 1.8 x 1.8	2.3 x 1.7 2.3 x 1.7		3.0 x 2.3 2.9 x 2.2	3.1 x 2.4 3.1 x 2.3		
J.10232	43	r 2.0 x 2.1 l 2.0 x 2.1	2.6 x 2.1 2.6 x 2.1	2.9 x 2.6 3.0 x 2.6	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	2.9 x 2.6 3.0 x 2.4	1.9 x 1.9 1.9 x 1.9	2.3 x 1.7 2.4 x 1.8		3.0 x 2.2 3.0 x 2.3	3.1 x 2.3 3.0 x 2.3		
J.6824	59	r l 2.0 x 2.0		3.8 x 2.7 3.8 x 2.8	3.0 x 2.7 3.0 x 2.5	2.9 x 2.6 2.9 x 2.4	2.9 x 2.6 2.9 x 2.4	2.9 x 2.6 2.9 x 2.4			3.8 x 2.6 3.7 x 2.5	2.9 x 2.3 2.9 x 2.3	3.0 x 2.3 3.0 x 2.3	2.8 x 2.2	
J.6826	59	r l		3.8 x 2.7 3.9 x 2.8	3.0 x 2.6 3.0 x 2.6	2.9 x 2.6 3.0 x 2.6	2.9 x 2.6 3.0 x 2.6	2.9 x 2.6 3.0 x 2.6			3.7 x 2.7 3.7 x 2.7	2.9 x 2.3 2.9 x 2.4	3.1 x 2.3 3.1 x 2.3	2.7 x 2.3	2.4 x 2.5 x
J.1145	61	r l		3.7 x 2.8 3.8 x 2.8	2.8 x 2.7 2.8 x 2.6	2.8 x 2.6 2.8 x 2.6	2.8 x 2.6 2.8 x 2.6	2.8 x 2.6 2.8 x 2.6			3.8 x 2.8 3.7 x 2.6	3.0 x 2.3 2.9 x 2.3	3.0 x 2.4 3.0 x 2.4	2.7 x 2.3 2.7 x 2.2	2.5 x 1.9 2.5 x 1.8
J.10233		r l		3.7 x 3.0 3.7 x 2.7	3.0 x 2.7 3.0 x 2.7	2.8 x 2.6 2.8 x 2.7	2.8 x 2.6 2.8 x 2.7	2.8 x 2.6 2.8 x 2.7			3.7 x 2.7 3.7 x 2.6	3.0 x 2.4 2.8 x 2.4	3.0 x 2.4 3.0 x 2.4	2.8 x 2.2 2.7 x 2.1	2.5 x 1.9 2.5 x 1.9
J.10234		r l		3.8 x 2.9 3.8 x 3.0	3.0 x 2.8 3.0 x 2.7	2.9 x 2.7 2.9 x 2.7	2.9 x 2.7 2.9 x 2.7	2.9 x 2.7 2.9 x 2.7			3.8 x 2.9 3.8 x 2.7	3.0 x 2.5 3.1 x 2.3	3.1 x 2.5 3.1 x 2.4	2.7 x 3.2 2.7 x 2.3	2.6 x 2.1 2.5 x 2.0
J.6822	65	r l		3.7 x 2.6 3.8 x 2.8	2.7 x 2.5 2.7 x 2.5	2.8 x 2.6 2.8 x 2.5	2.8 x 2.6 2.8 x 2.5	2.8 x 2.6 2.8 x 2.5			3.6 x 2.5 3.6 x 2.5	2.8 x 2.1 2.8 x 2.2	3.0 x 2.3 2.9 x 2.3	2.6 x 2.2 2.6 x 2.1	2.4 x 1.8 2.5 x 1.8
J.10235		r l		3.9 x 2.8 4.0 x 2.9	3.0 x 2.6 3.0 x 2.8	3.0 x 2.7 2.9 x 2.6	3.0 x 2.7 2.9 x 2.6	3.0 x 2.7 2.9 x 2.6			3.7 x 2.6 3.7 x 2.7	3.0 x 2.3 2.9 x 2.3	3.0 x 2.5 3.0 x 2.5	2.7 x 2.4 2.7 x 2.4	2.5 x 2.1 2.6 x 2.1
J.10236	68	r l		4.0 x 3.0 4.0 x 3.0	3.0 x 2.7 3.0 x 2.7	2.9 x 2.7 2.9 x 2.7	2.9 x 2.7 2.9 x 2.7	2.9 x 2.7 2.9 x 2.7			3.8 x 2.7 3.8 x 2.6	2.9 x 2.4 2.9 x 2.3	3.0 x 2.5 3.0 x 2.5	2.7 x 2.3 2.6 x 2.3	2.6 x 2.2 2.5 x 2.1
J.5932		r l		4.0 x 3.0 4.0 x 2.9	3.0 x 2.8 3.0 x 2.6	2.9 x 2.7 2.9 x 2.6	2.9 x 2.7 2.9 x 2.6	2.9 x 2.7 2.9 x 2.6			3.9 x 2.8 2.9 x 2.8	2.9 x 2.4 2.8 x 2.3	3.0 x 2.4 3.0 x 2.4	2.7 x 2.3 2.6 x 2.2	2.5 x 2.1 2.5 x 2.0
J.10237	66	r l		3.8 x 2.9 3.9 x 2.9	2.8 x 2.7 2.8 x 2.7	2.8 x 2.7 2.8 x 2.6	2.8 x 2.7 2.8 x 2.6	2.8 x 2.7 2.8 x 2.6			3.7 x 2.6 3.7 x 2.6	2.9 x 2.4 2.8 x 2.3	2.8 x 2.4 2.8 x 2.4	2.5 x 2.2 2.5 x 2.2	2.5 x 2.1 2.2 x 2.0



## Notes on the Skull

Cranium small, with maximum length of about 68mm.; elongate, with markedly tapering rostrum. Maxillae dorsally in considerable contact with frontals; laterally with infraorbital foramen often compound, with main (anterior) opening above anterior margin of P<sup>2</sup>; inferior process of anterior zygoma root weak; palate posteriorly with large vacuities, separated by narrow median septum. Palatines ventrally reduced to slender bar behind vacuities, forming two-thirds of median septum, and narrowly flanking posterior third of vacuities; dorsally in extensive contact in midline in roof of nasal passage, obscuring the presphenoid. Jugals laterally excavated, for superficial layer of masseter; zygomatic arches rather flattened, converging anteriorly. Roof of braincase gently arched; no sagittal crest, but old individuals have weak temporal ridges posteriorly confluent on well-developed interparietal. Squamosal anteriorly in narrow contact with frontal; subsquamosal foramen immediately above external auditory meatus; and prominent foramen just within meatus opening anteriorly to sinus in root of arch; no postglenoid process of squamosal. Tympanic tubular, but incomplete dorsally, and not smoothly uniting with squamosal in roof of meatus. Alisphenoidal bullae weakly inflated, in considerable contact with basioccipital, almost obscuring petrosal in ventral view; alisphenoid anteroventrally with small subvertical process extending to palatine and bounding pterygoid fossa. Paroccipital processes feebly developed. Supraoccipital inflated medially for vermis.

Mandible with ventral margin arcuate, greatest depth below M<sub>2</sub>. Symphysis ligamentary, elongate, extending to point opposite anterior of P<sub>3</sub>; postsymphysial swelling prominent. Diastemal crest conspicuous in lateral view. Masseteric canal deeply invading body of ramus, confluent with inferior dental canal; anterior margin of coronoid process thickened, ascending at about 50°. Angle broadly inflected, produced somewhat posteriorly towards margin. Condyle relatively low; articulating surface transverse, slightly convex longitudinally.

## THE SYSTEMATIC POSITION OF PROPLEOPUS AND HYPISIPRYMNODON

In the original description De Vis (1888) compared the type of *Trichis oscillans* with mandibles of species of *Hypsiprymnodon*, *Hypsiprymnus*, and *Phalangista*. He concluded that its affinities with *H. moschatus* were paramount, but suggested that "the Pleopodidae, embracing thus an ultimate stage of differentiation in *Hypsiprymnodon* and a more generalized type in *Trichis*, are a continuation of a stock whence had arisen the Phalangistidae on the one hand, the Hypsiprymnidae on the other". However, the pattern of tooth replacement and the development of the masseteric canal definitely establish the position of *Propleopus* and *Hypsiprymnodon* within the Macropodidae, in the current interpretation of this family; and there is no close relationship with any phalangerid genus.

The structure of the mandible of *P. oscillans* is closest to those of *H. moschatus* and species of *Bettongia*. In the relative shortness and heaviness of I<sub>1</sub>, the resemblance is to species of *Bettongia*. In the presence of a small, functionless I<sub>2</sub>, the length of the diastema, and the position of the mental foramen, the resemblance is clearly to *H. moschatus*. In the number of grooves of P<sub>3</sub>, its shape and size relative to the molars, the condition is closer to *H. moschatus*, but the degree of anterolabial deflection of its secant edge is intermediate between that of *H. moschatus* and *B. penicillata*. The

molar rows are straight as in *H. moschatus*, but slightly convergent anteriorly as in species of *Bettongia*. Molar gradation and cusp development are more comparable with the condition in *B. penicillata* and *B. gaimardi*, except that in *P. oscillans* the lophids are not so well developed and  $M_4$  is less reduced posteriorly; there is notable similarity in the production of the anterior cingulum labially beyond the forelink in lower molars and in the degree of anterior development of  $M_1$ . The great extent of the subhorizontal surface of wear of  $I_1$  in *P. oscillans* is a feature which cannot be matched in any related genus. It indicates comparable elongation of the crowns of  $I^2$  and  $I^3$ .

While *Propleopus* displays an intermediate condition in the development of several features of the mandible between that of *Hypsiprymnodon* and *Bettongia*, if size be disregarded, there is no uniform gradation and the separation of all three as distinct genera must be maintained. Individuals of *P. oscillans* far exceeded in size any of their living relatives; judging from the mandibular remains they must have been comparable in bulk to the living red and grey kangaroos. The species affords yet another instance of the climax of gigantism of terrestrial vertebrates on the Australian continent in the Pleistocene.

One consequence of the structural relationship of *Propleopus* with both *Hypsiprymnodon* and *Bettongia* is that the validity of the division of the rat-kangaroos into the subfamilies Hypsiprymnodontinae and Potoroinae becomes more questionable than ever. Tate (1948) maintained these as distinct subfamilies in his review of the classification of the Macropodidae, and associated *Potoroops*, *Potorous*, *Caloprymnus*, *Bettongia*, and *Aepyprymnus* in the Potoroinae. Previously Simpson (1945) had included both *Hypsiprymnodon* and *Propleopus* in the Potoroinae, without discussing the systematics of the group. On the other hand, Pearson (1946) had proposed the separation of the rat-kangaroos, including *Hypsiprymnodon*, as a distinct family, the Potoroidae, from the Macropodidae. He recognized the basic similarity in the structure of the female urogenital system in genera of his Potoroidae, and regarded its development in this group as more specialized than in the Macropodidae. Later Pearson (1950) maintained the Hypsiprymnodontinae and the Potoroinae as subfamilies of the Potoroidae.

Pearson's separation of the kangaroos into two families is based essentially on characters not utilized in the discrimination of other families of phalangeroid marsupials. It is contended that the presence of the basic body form including foot-structure; gait; skull structure, including the development of the masseteric canal; dental formula, and characteristic pattern of tooth replacement necessitates their grouping in the one family—the Macropodidae. The findings of Pearson however strongly support the division of the Macropodidae into two subfamilies, as in the classification of Simpson (1945).

From the description of the dentition it can be seen that the tooth change in *H. moschatus* conforms to the general pattern of the Macropodidae in that  $P_2^2$  resemble  $P_3^3$  in shape and function, are lost penecontemporaneously with the displacement of  $DP_3^3$  by  $P_3^3$  at a stage approaching adult body size,  $DP_3^3$  being more comparable in form with the true molars than the true premolars. The teeth mentioned are sometimes designated  $P_3^3$ ,  $P_4^4$ , and  $DP_4^4$  respectively by other authors. The views of Tate (1948) and Ride (1956) that *H. moschatus* is atypical in this regard are based on the work of Carlsson (1915). As was originally suggested to me in conversation by Mr. George Mack, Director of the Queensland Museum, Carlsson misinterpreted the anterior cheek teeth in the juvenile skull she examined. "Die beiden linken ausfallende Prämolaren" figured (1915, pl. 2, fig. 12) are in reality  $DP_3^3$  and  $M^1$  and the corresponding lower teeth (fig. 14) are  $DP_3^3$  and  $M_1$ . Apparently  $P_2^2$  had not yet erupted in the very young specimen studied (with skull length 24 mm.).

The brief coexistence of  $P^2$  and  $P^3$  in the tooth row of *H. moschatus* (fig. 2a) is due to the fact that while the crown of  $P^3$  is much longer than that of  $DP^3$ , it exhibits considerable axial deflection from the line of the cheek teeth on eruption.  $P_3^3$  are usually longer than  $DP_3^3$  in the Macropodidae and mechanically displace  $P_3^2$  and  $DP_3^3$  if the former have not been lost already.

Ride (1956) has already discussed in detail the resemblance between  $P_3^3$  ( $P_4^4$  of Ride) of *H. moschatus* and the phalangerid *Burramys parvus*. It is agreed that the occurrence of this type of sectorial in diverse mammalian groups renders specious any argument that its presence in these two marsupials is due to inheritance from a common ancestor rather than convergence.

It is commonly recognized that the presence of quadrituberculate crowns, which show, however, varying degrees of weak lophoid development, readily distinguishes the molars of the rat-kangaroos from the bilophodont structures of the Macropodinae. It is reasonable to assume that the Macropodidae were derived from omnivorous phalangerid ancestors with quadrituberculate molars. In the Macropodinae radiation has been towards browsing and grazing forms with bilophodont molars. In the rat-kangaroos, the trend, as reflected in the dentition, is incomplete, least of all in *Hypsiprymnodon*. The molar gradient, however, shows that *Hypsiprymnodon* is not an unmodified stem macropodid, but should be associated with the Potoroinae.

It may be argued that the presence of  $I_2$  in *Propleopus* and *Hypsiprymnodon* contributes a reason for the separation of these genera from the Potoroinae. In both cases the tooth shows only vestigial development, and in *Hypsiprymnodon*, at least, it may be interpreted as a relict structure in an animal whose diet and dentition show but little specialization beyond those of its ancestors. Such a structure is

useful in tracing phylogeny, but on the other hand its presence or absence need not be critical in any scheme of classification purporting to be consistent with that phylogeny.

Pearson (1950) has pointed out that the separation of the frontal and squamosal by the junction of the parietal seems to represent the primitive condition in the marsupial cranium. In addition he showed that this relation is maintained in the Macropodinae, but not in the rat-kangaroos, where *Hypsiprymnodon* shows divergence in the narrow contact of the frontal and squamosal, and the others greater deviation in the much wider junction of these bones.

As Abbie (1939) has demonstrated, the development of the masseteric canal in *H. moschatus*, in its confluence with the inferior dental canal, is comparable with the condition in the other rat-kangaroos. In the Macropodinae the masseteric canal, though extensive, merely opens into the inferior dental canal through a variously enlarged masseteric foramen. Comparison with the various developments of the posterior part of the mandible of phalangerids suggests that the structure of the masseteric canal in the Macropodinae is likely to be nearer the condition in the ancestral macropodids than that of the rat-kangaroos.

The lack of pronounced reduction of the fore-limb, the lack of pronounced elongation of the pes, especially the fourth digit, and the presence of the reduced hallux are three external characters which readily distinguish *H. moschatus* in appearance from its relatives. In determining their taxonomic significance, these structures can be considered collectively, in that they all relate to locomotion and less directly to food-gathering activity. *H. moschatus* is probably the only ground-dwelling phalangeroid marsupial with a strict rain-forest habitat. It is feasible that its early phalangerid ancestors were arboreal animals with a generally similar diet in a similar habitat. Other than limited divergence in the structure of the pes (and hind-limb as a whole), towards digitigrade modification, would have no adaptive significance in this habitat. It would appear that the trend towards specialized saltatory locomotion progressed outside this environment in forest and grassland areas, with concomitant specialization for herbivorous diets. Further, as the trend in limb development has apparently operated in both macropodid subfamilies, the retention of the primitive unspecialized condition in *H. moschatus* neither confirms nor denies its association with either group.

The naked tail in *H. moschatus* does not appear to be prehensile. Its adaptive significance may be that it is less likely to encourage parasites from the rain-forest floor.

Pearson (1946, 1950) has discussed the female urogenital system of the rat-kangaroos in detail. He demonstrated that they exhibit a marked specialization in several characters beyond the generally primitive condition in the Macropodinae,

and furthermore that the structure in *H. moschatus* conforms to the pattern of the group, with the exception that the fused median vaginal cul-de-sac is short and not produced posteriorly to reach the posterior vaginal sinus in parous adults. He used this as evidence in support of his view that *Hypsiprymnodon* is the most primitive genus of his Potoroidae.

#### CONCLUSION

The accumulated evidence indicates that in most of its characters which can be termed specialized, *Hypsiprymnodon* is comparable with the rat-kangaroos. Their development exceeds that of relative structures in the Macropodinae and shows that *Hypsiprymnodon* should not be considered as the surviving ancestral form for all Macropodidae, as maintained by Raven and Gregory (1946).

It is not disputed that in characters relating to diet and locomotion *Hypsiprymnodon* need show little specialization beyond the condition of hypothetical ancestral forms. Furthermore these generalized characters allow *Hypsiprymnodon* to be well adapted to its way of life in the rain-forest habitat. It is probable that this environment has been more stable over a longer period of time than other habitats, with less selection pressure than in the open forests and grasslands.

The classification of *Hypsiprymnodon* as a less specialized member of the Potoroinae is the more satisfactory one in terms of an analysis of the gross morphology and what can be inferred of the phylogeny. The genus may not have evolved far from the ancestral stock of the group, but the derivation of any particular genus from *Hypsiprymnodon*, such as *Bettongia* in the scheme of Bensley (1903), is beyond the available evidence.

*Propleopus* should also be included in the Potoroinae. The available characters of *P. oscillans*, which by comparison with those of the living forms are few in number, indicate that it stands closer to *Hypsiprymnodon* than any living genus does, but no direct line of relationship can be inferred.

The classification of the Macropodidae reverts to that of Simpson (1945). *Palorchestes*, separated in the subfamily Palorchestinae by Tate (1948), has been shown by Woods (1958) to belong to the Diprotodontidae. *Sthenurus*, with which *Palorchestes* was once associated in subfamily Sthenurinae by Raven and Gregory (1946), appears to be merely a macropodine form, specialized for browsing on coarse herbage. Both *Sthenurus* and the closely related genus, *Procoptodon*, need revision.

## LITERATURE CITED

- Abbie, A. A., 1939. A Masticatory Adaptation peculiar to some Diprotodont Marsupials. Proc. zool. Soc. Lond., ser. B, 109, pp. 261-279.
- Bensley, A., 1903. On the Evolution of the Australian Marsupialia; with Remarks on the Relationships of the Marsupials in General. Trans. Linn. Soc. Lond. (Zool.), ser. 2, 9, pp. 83-217, pls. 5-7.
- Carlsson, A., 1915. Zur Morphologie des *Hyposiprymnodon moschatus*. K. svenska Vetensk. Akad. Handl., 52, No. 6, pp. 1-18, pls. 1-3.
- De Vis, C. W., 1888. On an Extinct Genus of the Marsupials Allied to *Hyposiprymnodon*. Proc. Linn. Soc. N.S.W., 3, pp. 5-8, pl. 1.
- Etheridge, R., in Jaek, R. L., and Etheridge, R., 1892. The Geology and Palaeontology of Queensland and New Guinea. Brisbane, Government Printer, and London, Dulau & Co. XXXII+767 pp., 46 pl.
- Longman, H. A., 1924. Some Queensland Fossil Vertebrates. Mem. Qd. Mus., 8, pp. 16-28.
- Pearson, J., 1946. The Affinities of the Rat-kangaroos (Marsupialia) as revealed by a Comparative study of the Female Urogenital System. Pap. roy. Soc. Tasm. (1945) pp. 13-25.
- 1950. The Relationships of the Potoroidae to the Macropodidae (Marsupialia). Pap. roy. Soc. Tasm. (1949) pp. 211-229.
- Ramsay, E. P., 1876. Description of a new genus and Species of Rat Kangaroo, allied to the genus *Hyposiprymnus*, proposed to be called *Hyposiprymnodon moschatus*. Proc. Linn. Soc. N.S.W., 1, pp. 33-35.
- Raven, H. C., and Gregory, W. K., 1946. Adaptive Branching of the Kangaroo Family in Relation to Habitat. Amer. Mus. Nov., No. 1309, pp. 1-33.
- Ride, W. D. L., 1956. The Affinities of *Burrhamys parvus* Broom a Fossil Phalangeroid Marsupial. Proc. zool. Soc. Lond., 127, pp. 413-429, pls. 1-2.
- Simpson, G. G., 1945. The Principles of Classification and a Classification of Mammals. Bull. Amer. Mus. nat. Hist., 85, pp. 1-350.
- Tate, G. H. H., 1948. Results of the Archbold Expeditions, No. 59. Studies on the Anatomy and Phylogeny of the Macropodidae (Marsupialia). Bull. Amer. Mus. nat. Hist., 91, pp. 239-351.
- 1952. Results of the Archbold Expeditions, No. 66. Mammals of Cape York Peninsula with Notes on the Occurrence of Rain Forest in Queensland. Bull. Amer. Mus. nat. Hist., 98, pp. 565-616.
- Tedford, R. H., 1955. Report on the Extinct Mammalian Remains at Lake Menindee, New South Wales. Rec. S. Aust. Mus., 11, pp. 299-305.
- Woods, J. T., 1958. The Extinct Marsupial Genus *Palorchestes* Owen. Mem. Qd. Mus., 13, pp. 177-193.